FAUNISTIC SIMILARITY AND HISTORIC BIOGEOGRAPHY OF THE HARVESTMEN OF SOUTHERN AND SOUTHEASTERN ATLANTIC RAIN FOREST OF BRAZIL

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ABSTRACT. Harvestmen show a high degree of endemism in the Atlantic Rain Forest (eastern coast of Brazil). This biome shows the highest diversity of harvestmen inhabiting Brazil; 2/3 of the species are found in this area. Most of the species are distributed in a few thousand square kilometers, almost always within one mountain range. The similarities of 26 localities were studied, including sites from the Brazilian savanna, using data from recent collections (more than 8,000 specimens) and published data. A cluster analysis using Sørensens Coefficient indicated a high degree of endemism of species of harvestmen (similarity indexes below 0.5). It resulted in six main clusters related to the large mountain ranges and near sites. A high variation in richness was observed; 4–64 species per locality. The distribution of 84 species of four recently reviewed subfamilies of Gonyleptidae (Goniosomatinae, Caelopyginae, Progonyleptoidellinae and Sodreaninae) was studied. Eleven areas of endemism, with 3–14 endemic species each, were proposed. A primary Brooks Parsimony Analysis showed a possible first vicariant event splitting the fauna of two northern areas from the rest, and a second event splitting the fauna of southern areas (until 24°35″S) from those areas related to certain mountain ranges in the central Atlantic Rain Forest. The vicariant events were related to the uplifting of the Serra do Mar and the Serra da Mantiqueira, and the appearance of large rivers and climatic changes.

Keywords: Atlantic Rain Forest, biodiversity, Brooks Parsimony Analysis, harvestmen, Neotropics.

The Atlantic Rain Forest is located in the largest part of the Brazilian coastal region between 6-30° S, also occupying the central to southern interior part of the country. This biome comprises two types of vegetation formation: the Coastal Atlantic Rain Forest, close to the coast line, with elevations from sea level to approximately 1,000 m a. s. l., and with a hot, warm climate lacking a dry season; and the Atlantic Semi-deciduous Forest, which extends across the plateau in the interior of the country (usually above 600 m elevation), that can have a severe dry season, normally between April and September (Oliveira-Filho & Fontes 2000). The Atlantic Rain Forest was almost completely continuous in 1500, the year of the discovery of Brazil by Europeans, but is currently totally fragmented and reduced to less than 7.6% of the original area (Morellato & Haddad 2000). This occurred because colonization was mainly on the coast and most state capitals are in this biome. We

should stress that anthropogenic pressure is still strong on the remaining fragments. The few areas without or with a low anthropogenic pressure are in governmental reserves or in steep regions.

Diversity in the Atlantic Rain Forest seems to be higher than in most parts of the Amazonian Rain Forest, and endemism is remarkable; 50% on an average and as high as 95% in some groups of amphibians according to Morellato & Haddad (2000). However, such statements are mainly based on data for plants and vertebrates, the invertebrates remaining poorly studied. An examination of the records of Laniatores harvestmen of the Atlantic Rain Forest (see the catalog of Kury 2003) and Eupnoi (Tourinho-Davis & Kury 2003; Tourinho-Davis 2004) revealed that the group represents an exclusive fauna, with the highest level of endemism (97.5%) in this biome.

The opilionids are hygrophilous, have low vagility and are primarily nocturnal and cryp-

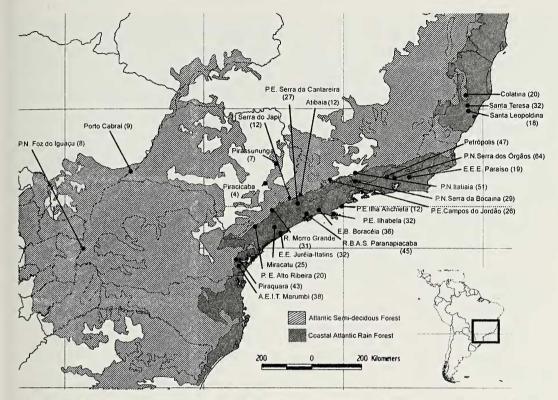


Figure 1.—Richness (between brackets) of Opiliones (Laniatores and Eupnoi) recorded in 26 localities in south and southern Brazil.

tic. Apparently the Laniatores possess low capability of dispersion. These aspects suggest the group is a good model for biogeographic studies. The only two studies dealing with opilionids which analyzed biogeography based on cladistic analysis were Briggs & Ubick (1989) and Ubick & Briggs (1989) for two genera of Laniatores, Phalangodidae, endemic to coastal California.

Few studies deal with historic biogeographic aspects of the Atlantic Rain Forest. Some studies related this biome as sister area with the Andean-Amazonian region (Amorim & Pires 1996) or as sister area with southern region (from São Paulo to Rio Grande do Sul) in case of groups with more southern occurrence in South America (Morrone et al. 1994; Pérez-Losada et al. 2004). A few biogeographic hypotheses based on phylogenetic reconstructions were proposed for the Atlantic Rain Forest, as the comprehensive studies of Costa (1995) for fishes and Amorim & Pires (1996) for dipterans and monkeys. The main goals of this article are to demonstrate the great diversity of opilionids in the Atlantic Rain Forest

including their high endemism, and to present a biogeographic hypothesis for the region.

METHODS

Similarity and richness.—The Sørensen index was applied to the analysis of similarity among the records of occurrence of 363 named species of Opiliones (Laniatores and Eupnoi) in 26 sites in south and southeastern Brazil. Morphospecies were not included because they were not standardized among all sites. The most intensively sampled sites were chosen, using the following criteria: more than 200 specimens collected; or stability or little increasing of richness with recent collecting. The analyses were performed with the MVSP 3.1 software (Kovach Computing Services 1999). The records were obtained from the literature (Laniatores from Kury 2003; Eupnoi from original descriptions and Tourinho-Davis 2004) in addition to museum records of the Museu de Zoologia da Universidade de São Paulo (MZSP), Instituto Butantan (IBSP) and Museu Nacional do Rio de Janeiro. These collections include old material and 8,879 specimens recently collected (2000–2004) for the project Biodiversity of Arachnida and Myriapoda of the State of São Paulo (IBSP, MZSP). The observed richness of each locality (Fig. 1) was calculated including morphospecies, records from literature and material from museums.

Biogeographic analyses.—Four subfamilies of Gonyleptidae, for which we have cladistic hypotheses at species level (Goniosomatinae, Caelopyginae, Progonyleptoidellinae and Sodreaninae), were used for biogeographic analyses. The areas of endemism were chosen by overlapping areas of distribution of at least three endemic species. The areas of endemism basically follow Pinto-da-Rocha (2002) with some modifications: the component Santa Catarina (SC) was split from Paraná (PR); the southern region of São Paulo (SSP), located in the Vale do Ribeira was split from the Serra do Mar of São Paulo; and the Serra dos Órgãos (Org) was split from the Serra do Espinhaço (SEsp). Other abbreviations are: Bahia (BA), Espirito Santo (ES), lowlands of the northern part of the São Paulo coast and the southern part of Rio de Janeiro state (LSRJ), Serra da Bocaina (Boc), Serra da Mantiqueira (Mnt), Serra do Espinhaço (SEsp), Serra do Mar de São Paulo (SMSP), and Serra dos Órgãos (Org).

The primary Brooks Parsimony Analysis (BPA) was performed to infer relationships among areas. In this analysis each terminal of the species' cladograms was replaced by the species' areas of distribution; terminals and nodes were transformed into a binary matrix (Brooks et al. 2001). The function of primary BPA is to determine whether there is a general pattern among areas (Brooks et al. 2001). Widespread taxa were considered informative and their area considered as monophyletic (Assumption 0). The matrix of the area was constructed with the patterns of distribution of 84 species (Table 1) of two species cladograms: one for the subfamily Goniosomatinae; and another for the monophyletic group composed of the subfamilies (Sodreaninae (Progonyleptoidellinae, Caelopyginae)). The hypotheses of relationship among subfamilies of Gonyleptidae and species of Caelopyginae are in Pinto-da-Rocha (2002). The revisions and hypotheses for the Goniosomatinae (M.B. da Silva and P. Gnaspini), Sodreaninae and Progonyleptoidellinae (both R. Pinto-da-Rocha) are in preparation for publication. Taxa cladograms (for species names see Table 1): Caelopyginae = (((7, 6)(2(4(3, 1))))) ((19(11)(10(12(13(18)) (14(15, 16, 17))))) (5(23(21(20, 22))) ((8, 9) (27(24, 25, 26)))))); Goniosomatinae = (((62, 63) ((50, 54) (64, 68)))((67(51, 55)) (73(66(52, 65))))) (((70(53(59, 65))))))75))) (60(57(49(56(61, 58))))) (82(84((79(80 (74, 78))) (77(83((71, 72) (81(69, 76))))))));Progonyleptoidellinae = ((45, 46)) ((48(47(41))(40,42))) (36(43, 44)(35(37(38(34, 39))))));Sodreaninae = (30(28(29(33(32, 31))))). The parsimony analysis of the biogeographic matrix was conducted with the PAUP 4.0 (Swofford 2002), using Branch-and-Bound algowith the commands hold10000, rithm mult*1000 and hold/1000.

RESULTS

Richness.—Richness varied from 4-64 species per locality in south and southeastern Brazil (Fig. 1). The areas of low diversity are in cerrado forests (Brazilian savanna) with 4-7 species (Piracicaba and Pirassununga) and in the Atlantic Semi-deciduous Forest with 8-12 species (Foz do Iguaçu, Porto Cabral, Japi and Atibaia). Localities in the Costal Atlantic Rain Forest are richer with 12-64 species. However, it must be stressed that some areas on the coast, such as Ilha Anchieta and Paraíso, were undersampled (40-50 h of nocturnal sampling) and there are no records either from literature or from museums. Thus, these estimates should be taken with care. Localities considered as well-sampled such as Cantareira, Morro Grande, Boracéia, Paranapiacaba, Itatiaia and Serra dos Órgãos, present 27-64 species. Therefore, the fauna of harvestmen of the Coastal Atlantic Rain Forest is richer than the Atlantic Semi-deciduous Forest and the cerrado.

Faunistic similarity.—Analyses showed clusters among localities of the same mountain range (Fig. 2). From the 363 species included in the matrix, 213 (58.7%) occurred in just one locality. Among the 150 species recorded in more than one locality, only 93 were in two. Therefore, the groups possess only a few species in common, generating very low indices of similarities, thus indicating the high level of endemism of harvestmen species.

The fauna of the Atlantic Rain Forest of the State of São Paulo forms a distinct group from other regions and also from the interior region

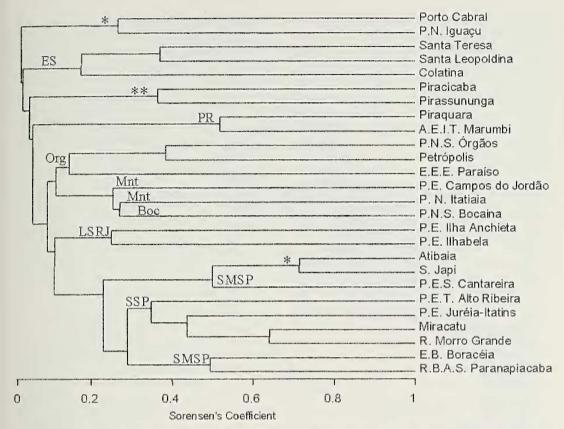


Figure 2.—Cluster analysis (Sørensen index) showing the similarity among harvestmen faunas (Laniatores and Eupnoi) of 26 areas in south and southern Brazil. Abbreviations in Table 1. * = areas not included in biogeographic analyses; ** = Cerrado (savanna).

of São Paulo (Cantareira, Japi and Atibaia). This group is divided into a cluster from the southern coast of São Paulo (Miracatu, Juréia, Morro Grande and PETAR), and another in the center of the São Paulo Coastal Rain Forest (Boracéia and Paranapiacaba).

A high similarity was found between the Serra do Japi (about 70%) and Atibaia, and can be explained by their proximity (ca. 30 km). The same occurs with the Paranapiacaba and Boracéia localities; besides their proximity, they belong to the same geomorphological formation. The fauna of the northern coast of the state of São Paulo is distinct from other regions of the State of São Paulo and even its two localities showed a low similarity (index below 0.30).

It is possible to identify a great cluster composed of localities of Serra do Mar of Rio de Janeiro, Serra da Mantiqueira and Serra da Bocaina. Within this cluster, the localities are even distinctly different from each other, the Serra do Mar of Rio de Janeiro, including the Serra dos Órgãos, formed a distinct subgroup from other localities, including Serra da Mantiqueira (Campos do Jordão and Itatiaia) and Serra da Bocaina. Other groups can be identified: localities of the cerrado (Piracicaba and Pirassununga); Serra do Mar of Paraná (Piraquara and Marumbi); Semi-deciduous Forest (P.N. Iguaçu and Porto Cabral); and a group formed by three localities in Espírito Santo.

Historical Biogeographic Analysis.— Among the 84 species included in the analysis, 66 occur in one area, 13 were recorded in 2–3 areas, four in 4–8 areas and two have no precisely known locality (Table 1). The studied groups were not recorded in the cerrado and the more interior areas of the Atlantic Semi-deciduous Forest, except for the Mnt and the SEsp. Eleven areas of endemism were recognized as having at least three endemic species belonging to the subfamilies Caelopyginae, Goniosomatinae, Progonyleptoidellinae and Sodreaninae (Fig. 3). Primary BPA

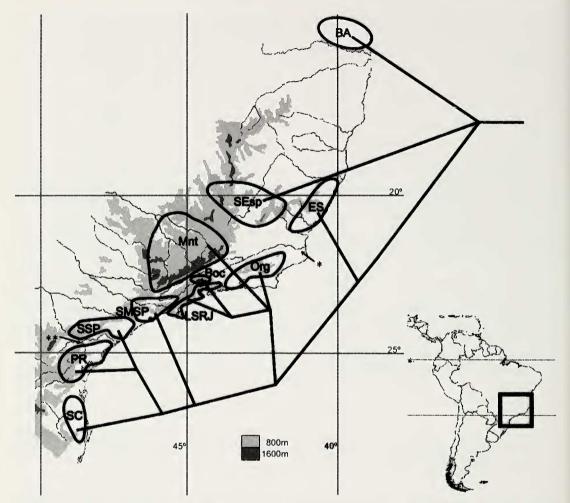


Figure 3.—Strict consensus area cladogram of harvestmen subfamilies Caelopyginae, Goniosomatinae, Progonyleptoidellinae and Sodreaninae (Gonyleptidae) based on three equally parsimonious trees (L = 248; CI = 0.66; RI = 0.57). Abbreviations of names in Table 1; * = Paraiba do Sul River; ** = Ribeira do Iguape River.

analyses resulted in three equally parsimonious cladograms (L = 248; CI = 0.66; RI =0.57) and the strict consensus (L = 254; CI = 0.64; RI = 0.54) is shown in Fig. 3. The three cladograms varied in positions of BA and SEsp, which formed a group in two cladograms, SEsp being more related to other areas than to BA in the third cladogram. The placement of Org and Mnt also varied, with the Org sister of Boc+LSRJ being in two cladograms and Mnt sister of the Boc + LSRJ in one. The consensus cladogram shows a sequence of vicariant events from North to South. However, it should be noted that the basal position of Bahia and Serra do Espinhaço in the cladogram could be due to the few endemic species recorded in these areas besides the insufficient information to relate them to the southern areas, such as Serra do Espinhaço. The vicariant events that followed separated Espirito Santo from the southern areas and the central areas of São Paulo, and Rio de Janeiro from the southernmost areas. The Serra do Mar of the State of São Paulo was split from the continuous remaining part just south of São Paulo, as this area showed affinities with southern Brazil from which it is separated by the Ribeira do Iguape River.

DISCUSSION

Brazil harbors about 900 species of harvestmen (see Kury 2003 and Hallans catalog

at http://entowww.tamu.edu/research/collection/hallan/OpilRpt2.txt). The Coastal Atlantic Rain Forest possesses most of this diversity (about 600 described species), which makes this area the most diverse in the world for this taxonomic group. Among the 16 subfamilies of Gonyleptidae, the predominant group in the Atlantic Rain Forest, nine are exclusively found in this vegetation formation, whereas two occur mainly in this region (Tricommatinae and Hernandariinae). These 11 subfamilies include 223 described species. Other diversified groups found in this region are Pachylinae, Gonyleptinae and Sclerosomatidae, among others.

The study of similarity patterns (Fig. 2) among the well-sampled localities (Fig. 1) showed an almost total coincidence with the areas of endemism herein proposed. The very low similarity between localities and groups of localities show how isolated these faunas are. These results indicate the high influence of geomorphology and geographical isolation in the pattern of harvestmen species distribution. The clusters show, in general, that localities in the same mountain range are more similar to each other than to those in other mountain ranges.

There are two main biogeographic studies in South America that consider south and southeastern Brazil as belonging to more than one biogeographic component. Costa (1995) presented an area cladogram for three groups of Cyprinodontiformes, 23 other groups of fishes, and one genus of frog. Amorim & Pires (1996) presented a general area cladogram based on several groups of neotropical dipterans (Ditomyiidae, Sciaridae and Scatopsidae) and monkeys (Callitrichidae). Both hypotheses considered the Atlantic Rain Forest as having 4-6 components. However, the vicariant events postulated by these authors considered different areas of endemism for terrestrial and freshwater animals. Biogeography of the freshwater fauna seems to be related to paleodrainages that flowed to the interior or the Atlantic Ocean (Lundberg et al. 1998). On the other hand, the terrestrial fauna occurs on both sides of the mountain range. Costa (1995) suggested that the coastal areas form a component that is sister to a biogeographic component (his area "f") that encompasses a large interior region around the La Plata and São Francisco Basins, and includes our area BA. In his study, the components of the Serra da Mantiqueira and the Serra do Espinhaço do not possess any taxa. According to Costa (1995), the coastal components share a unique ancestral area in which the first vicariance event split areas "i+h" from "g" (similar to our areas SMSP, LSRJ, Boc, Org, and ES), followed by a second divergence between his areas "i" (with no taxon in our study), and "h" (our SC, PR e SSP). Amorim & Pires (1996) related SE Amazonia with other Brazilian regions. According to them, the areas comprising the center and northeast sections of Brazil (areas MGBA and NEBr in their fig. 26) form a component which is sister to southeast Bahia (our BA). This whole component is sister to a clade comprised of north Rio de Janeiro (our ES), São Paulo-Rio de Janeiro (our Org, Mnt, Boc, LSRJ, SSP, PR and SC), and southern Brazil and the northeast of Argentina (areas for which there are no opilionids related to this study).

The main vicariant events are related to mountain uplift and the appearance of valleys. The origin of the Serra do Mar and the Serra da Mantiqueira was during the Paleocene (Petri & Fulfaro 1988), or early in the Upper Cretaceous, as a result of tectonic activity (Almeida & Carneiro 1998). Although the great orographic ascension occurred between the Pliocene and the Pleistocene, we should stress the origin as being recent. Valleys seem to represent important geographical barriers, such as the valley of the Paraíba do Sul River, whose origin was during the Oligocene-Miocene (Petri & Fulfaro 1988), and isolated the Serra da Mantiqueira in the west from the Serra do Mar, Serra da Bocaina and the Serra dos Órgãos in the east. In addition, the same valley isolated the northern areas (Espírito Santo, Serra do Espinhaço and Bahia) from the remaining southern ones (Fig. 3).

It is interesting to note that the Atlantic side of most coastal mountains receives a large amount of rain (up to 4,000 mm a year). On the other hand, the interior side is in a rain shadow, and a valley such as Paraíba do Sul, receives one-third as much rain as the adjacent mountain range (Behling & Lichte 1997). Another remarkable fact was the generation of new environments during glaciations in the Pleistocene, such as grasslands and short gallery forests, in areas previously covered by rain forests, where currently there are semi-

Table 1.—Distribution of species of harvestmen subfamilies Caelopyginae, Goniosomatinae, Progonyleptoidellinae and Sodreaninae (Gonyleptidae) in eleven areas of endemism in south and southeastern Brazil. SC = Santa Catarina; PR = Paraná; SSP = Sul de São Paulo; SMSP = Serra do Mar de São Paulo; Mnt = Serra da Mantiqueira; Boc = Serra da Bocaina; LSRJ = north coast of São Paulo and south of Rio de Janeiro; Org = Serra dos Órgãos; ES = Espírito Santo; SEsp = Serra do Espinhaço; BA = southern coastal Bahia.

Species/area	SC	PR	SSP	SMSP	Mnt	Boc	LSRJ	Org	ES	SEsp	BA
Caelopyginae											
1. Ampheres fuscopunctatus				X			X				
2. A. leucopheus		X	X	X	X	X	X	X	X		
3. A. luteus					X						
4. A. tocantinus	?	?	?	?	?	?	?	?	?	?	?
5. Arthrodes xanthopygus								X			
6. Caelopygus elegans								X			
7. C. melanocephalus								X			
8. Garatiba bisignata							X				
9. G. bocaina						X					
10. Metarthordes albotaeniatus									X		
11. M. bimaculatus									X		
12. M. hamatus								X		X	
13. M. laetabundus						X		X			
14. M. leucopygus									X		
15. M. longipes				X			X				
16. M. nigrigranulatus					X	X		X			
17. M. pulcherrimus				X							**
18. M. xango											X
19. Metampheres albimargina-								37			
tus								X			
20. Pristocnemis albimaculatus				37		v	v	X			
21. P. farinosus				X	v	X X	X	X			
22. P. perlatus		X	Х	X	X X	X	X	X			
23. P. pustulatus 24. Thereza albiornata		Λ	Λ	Λ	Λ	Λ	Λ	Λ	X		
25. T. amabilis							X		Λ		
26. T. poranga							X				
27. T. speciosa	X	X					28				
	Λ	Λ									
Sodreaninae											
28. Gertia hatschbachi		X									
29. Sodreana sodreana			X	X				X			
30. Stygnobates barbiellinii							X	**			
31. Zortalia bicalcarata	**							X			
32. Z. inscripta	X	**	37				37				
33. Z. leprevosti		X	X				X				
Progonyleptoidellinae											
34. Cadeadoius niger		X									
35. Gonyleptoides acanthoscelis								X			
36. G. curvifemur				X							
37. G. marumbiensis		X									
38. Heliella singularis		X									
39. Iguapeia melanocephala		X	X								
40. Iporangaia pustulosa			X								
41. Leptocnema sulphurea								X			
42. Mitopernoides variabilis							X				
43. Moreiranula mamillata				X							
44. M. moreirae					X						

Table 1.—Continued.

Species/area	SC	PR	SSP	SMSP	Mnt	Boc	LSRJ	Org	ES	SEsp	BA
45. Progonyleptoidellus fuscop-											
ictus				X							
46. P. striatus			X	X							
47. Gen. sp.n. 1							X				
48. Gen. sp.n. 2						X					
Goniosomatinae											
49. Acutisoma banhadoae		X									
50. A. discolor							X				
51. A. hamatum					X						
52. A. indistinctum										X	
53. A. inerme	X										
54. A. inscriptum							X				
55. A. longipes					X						
56. A. molle		X									
57. A. proximum		X	X	X							
58. A. thalassinum	X										
59. A. sp.n. 1		X									
60. A. sp.n. 2	X										
61. A. sp.n. 3			X								
62. A. sp.n. 4						X					
63. A. sp.n. 5				X							
64. A. sp.n. 6						X					
65. A. sp.n. 7											X
66. A. sp.n. 8					X						
67. A. sp.n. 9				X							
68. Goniosoma albiscriptum				X							
69. G. calcar								X			
70. G. catarina	X										
71. G. dentipes								X			
72. G. ensifer								X			
73. G. modestum											X
74. G. roridum								X			
75. G. spelaeum			X		**	**	77	3.7			
76. G. unicolor					X	X	X	X		**	
77. G. vatrax								3.7		X	
78. G. venustum								X	*7		
79. G. varium								X	X		
80. G. sp.n. I								v	X		
81. G. sp.n. 2							37	X			
82. Gen n spn							X				
83. Lyogoniosoma macracan-					37						
thum					X					W	
84. Xulapona cara										X	
Species/area	SC	PR	SSP	SMSP	Mnt	Boc	LSRJ	Org	ES	SEsp	BA
Total species	6	13	10	15	11	10	16	23	7	4	3
Endemic species	5	7	3	7	6	4	9	14	5	3	3

deciduous forests as in the interior of the State of São Paulo (Behling & Lichte 1997) or low-lands as is the case in the State of Santa Catarina (Behling & Negrelle 2001; Behling 2002). The replacement of rain forest by less

plant diverse and more open environments could have decreased the diversity of opilionids in those sites. The tree floras of semi-deciduous forests are less diversified than coastal forests, so they have been considered a subgroup of the former (Oliveira-Filho & Fontes 2000). However, this difference is not as remarkable as it is in harvestmen. Nevertheless, we should stress that only two areas of the semi-deciduous forests were well sampled (Serra do Japi and Atibaia). This characteristic could lead to a misunderstanding of the relationships between coastal and interior areas. The high diversity of opilionids in the Coastal Atlantic Rain Forest, an area of higher diversity than any other country in the world, can be explained by the high number of geographical barriers on the Brazilian coast that isolated populations creating new species, and also by many events of forest fragmentation, hence leading to population divergence, due to climatic changes during the Pliocene-Pleistocene.

The unique opilionid faunas represented in each of the 11 areas of endemism call attention to the necessity of preserving those environments. The Atlantic Rain Forest is a hotspot, and the decimation of the Brazilian Atlantic Forest is one of the most alarming conservation problems in the world (Terborgh 1992). This biome possesses a great number of protected areas along the coast in the southsoutheastern part of Brazil. In fact, most collecting was done in reserves. However, the opilionid faunas of three areas of endemism (ES, SEsp and BA) are poorly or not represented in terms of governmental reserves (see Conservation International do Brazil 2000 or the online atlas at http://www.sosmatatlantica. org.br/?secao=atlas), and their remaining habitats are suffering high anthropic pressure (Morellato & Haddad 2000), and deserve better attention in future planning of new protected areas in order to maintain the diversity of the group.

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